

Baker's Law and Dioecism in the Hawaiian Flora: An Apparent Contradiction

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ABSTRACT: Much evidence available in the literature supports the contention of H. G. Baker that self-compatibility is the rule in plants which have undergone long distance dispersal. However, in the Hawaiian flora there may be a high incidence of dioecism which represents an extreme form of outbreeding. Data are compiled which support the viewpoint of a higher than continental incidence of dioecism in the Hawaiian flora. A simple explanation is advanced for resolving the apparent contradiction between the higher percentage of dioecism and the isolation in the Hawaiian flora.

A HIGH DEGREE of self-compatibility is evidenced in plants which have undergone long distance dispersal (Baker, 1953, 1955, 1959*a*, 1959*b*). Stebbins (1957) suggested the term "Baker's Law" for this type of response to selection by the establishment of a closed breeding system. Self-compatibility which permits inbreeding increases the chances for a few individuals to establish themselves in an area new to their population. On the other hand, if they are subject to enforced outcrossing because of either a self-incompatibility mechanism at the chemical level (Baker, 1948) or because of the dioecious habit there would be less chance for success in establishment. This interpretation is well stated by Davis and Heywood (1963:376) under the heading, Long-Distance Dispersal: "Clearly if it is an inbreeding individual it will have a much better chance of being fertilized in the absence of pollen from another individual and of building up a new colony, than if it were an outbreeder depending on other individuals for pollen." Baker (1953) also makes the point that self-compatible species are not dependent upon insects for pollination, which insects might not be present in the new area.

Baker (1955) cites some examples where selection apparently has acted in preserving a self-compatible species which has been dispersed over long distances. Taylor (1954) studied the flora on Macquarie Island, a small

isolated sub-antarctic island. He recorded thirty-five species of vascular plants, three of which are endemic. Recourse to the available geological information indicated to Taylor that the island had been completely covered by ice during the Pleistocene epoch. Therefore, the plants must have arrived sometime after the Pleistocene. He suggests that the three endemics have evolved *in situ* and notes that one of these, *Coprosma pumila* (Rubiaceae), is dioecious elsewhere in its range but on Macquarie Island is mainly monoecious.

An example of self-compatibility and long distance dispersal is available in the animal kingdom. Longhurst (1955) reports successful long distance dispersal in a self-fertilizing crustacean, *Nostostraca*. He feels that this small crustacean has spread so successfully because of its characteristic small, light, easily dispersed eggs that do not hatch unless they are first subject to desiccation and because of their self-fertilizing habit.

Grant (1958) has found that many California annuals with self-incompatibility are represented in the Great Basin and other outlying areas by self-pollinating forms. Further evidence for Baker's Law is provided by the strand flora in Hawaii. It is generally accepted that strand plant species throughout the world are distributed by means of long distance dispersal. Indirect evidence for this is provided by McCaughey (1918). He estimates that of the littoral flora in the Hawaiian Archipelago, 30 per cent are endemic. His category, littoral, is in no way comparable to strand, including many more

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species at great distances from the shore. Nevertheless, he found that only 30 per cent are endemic. This can be compared with the approximately 80 per cent endemics which have been estimated for the entire Hawaiian flora (St. John, 1946; Hillebrand, 1888). A more recent estimate (Stone, 1967) is that specific endemism could amount to about 96 per cent. This bespeaks rather continuous arrival of strand species by long distance dispersal. The percentage of dioecism in strand plant species from some low Pacific islands to the west of Hawaii was estimated by Long (1965, personal communication). Long concludes that less than 1.0 per cent of the strand plant species with which he is familiar are dioecious. The evidence from McCaughey (1918) supports the consensus that most strand plants have reached the shores upon which they are established by means of long distance dispersal. Long's estimates support the contention of Baker that long-distantly dispersed species are self-compatible.

In dealing with self-compatibility and dioecism it must, of course, be kept in mind that dioecism is not the only mechanism for producing outcrossing. However, it is easier to recognize self-incompatibility at the level either of dioecism or heterostyly than at the chemical level of self-incompatibility. Just because a species does *not* show dioecism is no indication that it does not have other mechanisms providing for outcrossing. Nevertheless, dioecism percentage does give an indication of percentage of outcrossing. Baker (1959a:181) writes, ". . . We might expect that the proportions of hermaphrodite species relative to those with separate staminate and pistillate flowers (particularly the dioecious species) will give at least a very crude indication of the prevalence of outcrossing."

An assumption which is fundamental to Baker's Law is that species that show a higher percentage of one breeding system under one set of conditions can change to another breeding system under a different set of conditions. Davis and Heywood (1963), Grant (1958), and Fryxell (1957) have emphasized that the degree of outcrossing in the same species may vary under different conditions from as much as 50 per cent to as low as 2-3 per cent such as occurs in cotton. In support of this is the

experimental work of Jones (1932, 1934) who was able to produce a dioecious strain of *Zea mays* from a monoecious strain. A dioecious species of *Mussaenda* (Rubiaceae) appears to have evolved from a heterostylous form. Ornduff (1966) states that dioecism has probably arisen from heterostyly in the Menyanthaceae. Taylor's (1954) observations on *Coprosma pumila* provide another example.

There seems to be abundant support both theoretical and observational for the thesis so well expounded by Baker that the breeding system is of the utmost importance in successful long distance dispersal. There is a clear relation between self-compatibility and long-distantly dispersed species. This is made possible because breeding systems are dynamic. The breeding system can change in a given species when there is selection for self-compatibility, as, for example, in an area where only a few individuals of a given population are present. This seems to occur, both toward the margins of a population's distribution and also in totally new areas which are attained by long distance dispersal.

DIOECISM IN HAWAII

Accepting the validity of Baker's Law, the question arises of how to explain the high degree of dioecism in the Hawaiian flora. Dioecism is certainly an outcrossing breeding system, and the Hawaiian Islands are isolated. The origin of the flora can be explained in one or both of the two possible ways: either (1) there has in the past been closer connection with other land masses, or (2) the plants arrived by long distance dispersal. Before attempting to show how Baker's Law can be equated with the high degree of dioecism in the Hawaiian flora, let us see if there actually is a high degree of dioecism relative to a continental flora.

Observations of botanists who have worked on continental floras and also that of Hawaii have led them to suspect that Hawaii has a disproportionate number of dioecious species (Carlquist, 1965, 1966a, 1966b). Tabulations of the dioecious species for the Hawaiian flora were made using Hillebrand's *Flora of the Hawaiian Islands* (1888), and for a continental flora using Munz's *Manual of Southern California Botany* (1935). Admittedly the sample which

I obtained for the circumscribed area in southern California is more complete than that for the Hawaiian Islands since a considerable number of species have been added to the indigenous Hawaiian flora as new discoveries of species were made since 1888. A much smaller number of additional indigenous species have been added to the flora of California since 1935. Nevertheless, Hillebrand's *Flora* is relatively complete. He included slightly more than 700 species among the indigenous phanerogams of Hawaii. St. John (1946) estimated that the indigenous phanerogams in Hawaii included 1,795 species and infraspecific taxa. If the species only are considered, it is very likely that there would be fewer than 1,200. The number of dioecious species in Hawaii (based on Hillebrand, 1888) and that of southern California (Munz, 1935) are compared in Table 1. Also compared is a bare representation of the flora of Ecuador, a tropical continental flora, the data for which are based on Diels' report (1938) of several months' collecting and include a total of only 658 species. This must represent a very small portion of the entire flora. Furthermore, Diels probably included a disproportionate number of species from the alpine region of the Andes where he spent more of his collecting time. Therefore, some reservations should be held in comparing the data on the flora from Ecuador with those of the other two floras. However, this information is included because it represents, perhaps poorly, both a tropical flora (as does the Hawaiian) and a continental flora (like that of southern California).

Table 1 indicates that the percentage of

dioecism for the southern California flora is about 3 per cent and that of the Hawaiian flora about 5 per cent. This can be compared with figures of Yampolsky and Yampolsky (1922) which show 5 per cent complete dioecism for flowering plants of the entire world. If the number of dioecious species among the Hawaiian flora is incorrect it is very likely that the error was in underestimating dioecism. Hillebrand often was forced to describe species on the basis of inadequate specimens collected by someone else, and perhaps accompanied by poor notes. Thus, he was not always able to state whether a species was dioecious, monoecious, or hermaphroditic.

In compiling the data for Table 1, only those species clearly described as "dioecious" were included in that category. The percent of dioecism might have been higher if gynodioecism had been included. It is therefore safe to assume that the proportion of dioecious species in the Hawaiian flora is at least 5 per cent and very likely higher. The estimate of dioecism for the continental, temperate flora of southern California, as obtained from Munz's *Manual*, is probably much more accurate, and indeed it compares well with the estimate of Baker (1966, personal communication) for all of California—2.4 per cent. A two-by-two contingency table, chi square test for homogeneity was made for a comparison between dioecism in the two study areas, southern California and Hawaii. The results show that the difference in ratios is significant ($P < .005$). It is therefore extremely likely that a real difference exists in the amounts of dioecism in the two floras.

TABLE 1

COMPARISON OF THE TOTAL NUMBER OF
INDIGENOUS ANGIOSPERM AND GYMNOSPERM
SPECIES IN THREE AREAS AS
RELATED TO DIOECISM¹

AREA	TOTAL SPECIES	DIOECIOUS SPECIES ²	PER CENT DIOECIOUS
Hawaii	730	39	5%
So. Calif.	2,335	67	3%
Ecuador	658	20	3%

¹ Data compiled from Hillebrand (1888) for Hawaii, Munz (1935) for southern California, and Diels (1938) for Ecuador.

² Only those species which are listed as dioecious are included; polygamous or gynodioecious forms are not included.

DIOECISM AND WOODY HABIT

A comparison was then made to determine whether the difference in percentage of dioecism in the two areas might merely reflect the higher proportion of woody species in all tropical floras. Woody species are never annuals, and annuals do not usually have any sort of outcrossing mechanism. Baker (1959a) emphasized the point that there is a close association between outcrossing and perennial habit. Trees generally show outcrossing and heterozygosity (Baker, 1959a).

Table 2 presents the results of the compari-

TABLE 2
COMPARISON OF DIOECISM AND WOODYNESS IN THE FLORA OF THREE AREAS¹

AREA	TOTAL SPECIES	WOODY SPECIES	PER CENT WOODY OF TOTAL	WOODY AND DIOECIOUS	PER CENT DIOECIOUS OF WOODY SPECIES
Hawaii	730	325	44%	32	9%
So. Calif.	2,335	613	26%	22	3%
Ecuador	658	282	42%	19	7%

¹ Data compiled from Hillebrand (1888) for Hawaii, Munz (1935) for southern California, and Diels (1938) for Ecuador.

sons between woodiness and dioecism in the three areas, Hawaii, California, and Ecuador. This comparison exposes an even greater difference between the floras of Hawaii and California. Based on the total number of woody species that could be tabulated from Hillebrand's *Flora* and the number from Munz's *Manual*, the percentage of those showing dioecism is 3 for California and 9 for Hawaii. The two-by-two contingency table indicates a significant difference ($P < .005$). The percentage of woody species showing the dioecious habit in the Hawaiian flora is so much greater than that in the Californian flora that one can be assured that some factor is responsible for the difference. It could not be merely random chance.

Our question—Is there a significantly higher percentage of dioecious species in the Hawaiian flora than in a continental flora?—can be answered in the affirmative on the basis of the samples from Hawaii and from southern California. Relative to the comparison of the percentage of dioecism in woody species in Hawaii and in Ecuador, the difference, while less, is still significant ($P = .005$). It is of interest to compare the present results with estimates of percentage dioecism from some other areas. Baker (1966, personal communication) has calculated that the approximate percentage of dioecious species in west tropical Africa was 3.2 per cent and for all of California, 2.4 per cent. Parsons (1958) found approximately 3.9 per cent dioecism for the Angiosperms of Australia. Milliner (1966, personal communication) estimated that approximately 20 per cent of the indigenous flora of New Zealand was dioecious.

EVOLUTION OF DIOECISM IN HAWAIIAN PLANTS

The problem remains of explaining why there is a higher percentage of an outcrossing

type of breeding system (dioecism) in Hawaii, an area that apparently can be attained only by long distance dispersal. The possibility of an alternative explanation for the origin of the Hawaiian flora will be discussed briefly later. Let us assume that at least a majority of the indigenous species now present either have arrived themselves by long distance dispersal or have evolved from ancestors that had arrived in this way. This is the more likely explanation. Fosberg (1948) suggests that if on an average one seed plant arrived and became successfully established every 20,000 to 30,000 years the present flora would be accounted for. His calculations are based on the number of indigenous species now present and the estimate of ". . . 5–10 million years of above-water history for the entire Hawaiian chain." This estimate is in line with the ones given today by geophysicists (Woollard, 1965) who suggest that the youngest island may be about 2 million years old and the older islands about 5 million years old.

To explain this *apparent* contradiction between Baker's Law and high dioecism in Hawaii the author believes that the dioecious species present have evolved this habit *in situ* and are descended from species or strains that were hermaphroditic when they arrived and became established. That there has been time for this sort of change to dioecism to occur is evident. Approximately 80 per cent of the Hawaiian flora consists of endemics (St. John, 1946). These endemic species had time to evolve. Dioecism can occur quite rapidly. Jones (1932, 1934) experimentally produced a dioecious maize in four generations. Warmke and Blakeslee (1940) established a dioecious tetraploid race in a species of *Melandrium* (= *Lychnis*, Caryophyllaceae). H. Lewis (1966) has pointed out that differences in chromosome numbers between members of the same family in differ-

ent areas may be the result of saltational speciation. That short term dioecism can occur very quickly is undeniable. This type of dioecism is present according to D. Lewis (1942) in those families that have only a few dioecious members. He feels that the majority of dioecious species show the short term type of dioecism that is controlled by few genes and is reversible, and he postulates that it is only within families like the Salicaceae that dioecism is irreversible. Yampolsky and Yampolsky (1922) estimated that about 75 per cent of all the families of the phanerogams have some dioecious species.

The percentage of families with dioecious species does not differ appreciably in the two study areas, Hawaii and southern California, being approximately 15 and 14 per cent respectively. In comparing these percentages with the estimate of 75 per cent by Yampolsky and Yampolsky (1922) caution is indicated in drawing conclusions. In neither of these two floras does the distribution of dioecious species per family seem to reflect the distribution for families of the world. While this could simply indicate that the sample in regard to species per family is inadequate here, it could also indicate that factors are at play in both these floras which are not generally found throughout the world.

If it is true that dioecism has largely, if not totally, evolved *in situ* in the indigenous dioecious species of the Hawaiian Islands, and the evidence is strong that it has, why has selection acted favorably toward dioecism? The answer would be that dioecism is a very effective mechanism for insuring outcrossing. Outcrossing produces heterozygosity, and heterozygosity provides more potential recombination types. In a small population, such as would exist shortly after the arrival and establishment of long-distantly dispersed species, the gene pool would be relatively small. Additional genotypes coming in from other populations would be rare indeed. A factor which favored outcrossing and the concomitant greater variability would probably be selected for. Lewis (1942) and Grant (1958) both have emphasized that the genetic system and its controlling factors are themselves subject to evolution. The factors making up a genetic system include mutation rate, chiasma frequency, meiosis, fertility, and, of course, the breeding system.

Whitehouse (1950), in emphasizing the importance of outbreeding to adaptation, has also suggested that when species are once adapted to a given situation the outbreeding mechanism may then be lost. Some current workers, studying small populations, seem to feel that self-pollination systems will be selected for and retained. Moore and Lewis (1965:113) write, "In a very small population genes promoting self-pollination would be at an advantage. Once established, an inbreeding race would become self-perpetuating." Apparently, however, if the selection pressure is great enough, the inbreeding system need not be self-perpetuating. Such a situation with strong selection pressure for an open recombination system would exist in the Hawaiian flora. The Hawaiian Islands include in a small area a large number of very different habitats. These habitats may change quickly because of the high rainfall producing landslides and because of volcanic effects. Different ecological niches are suddenly made available in such a situation. Baker (1953) has emphasized the greater advantage that an outbreeder has over an inbreeder in occupying a new niche.

DISCUSSION

The present author maintains, therefore, that selection pressure for an outcrossing breeding system has been very strong in Hawaii and has resulted in the survival of a higher percentage of dioecious species and survival of a lower percentage of hermaphrodite species, than are found in the North American continent. In the tropical continental flora there may be almost as high a percentage of dioecism as in Hawaii. The evidence is too flimsy to attempt to draw any conclusive comparisons between a continental tropical flora and an insular tropical flora. However, it would not be too surprising to discover that a flora such as that in Ecuador actually did show a percentage of dioecism somewhere between that of an insular tropical flora such as Hawaii and that of a continental temperate flora such as California. One would expect that in a continental tropical flora the selection pressure for dioecism, an outcrossing breeding system, might be less than in an isolated flora such as in Hawaii with a tropical climate and yet somewhat more than in a

temperate flora with a less changing landscape. The rainfall of southern California is such that landslides though they occur are not the rule. This is quite the opposite of the situation generally found in the tropics.

The foregoing interpretation has been based on the assumption that the flora of Hawaii has developed largely from species which arrived through long distance dispersal. Campbell (1919, 1933) felt that the Hawaiian Archipelago is a remnant of a much larger area which was once in more or less direct connection with the South Pacific. He maintained that the isolation occurred in early Tertiary and that the older genera are derived from the South Pacific before isolation, and that the younger genera such as those belonging to the Compositae arrived after isolation by long distance dispersal and largely from the east.

Skottsberg (1925) proposed that the flora of Hawaii represents the derivatives of an ancient antarctic continental flora. He speaks of a "Jurassic Hawaii" and apparently felt that such did once exist. The hypothesized sub-antarctic continent of Skottsberg and pre-Tertiary central Pacific land mass of Campbell are interesting conjectures. However, even if one assumes that they did occur, the Hawaiian Archipelago has been isolated for at least 5,000,000 years. Fosberg (1948) indicated that 5-10 million years would be enough time to account for the present flora, assuming one arrival by long distance dispersal on an average of once every 20,000 years.

If there is a high proportion of outcrossing in the species of the Hawaiian flora one would expect to find many polymorphic species. As Baker (1953) has pointed out, in outbreeding populations there is an almost continuous intergradation between different populations while in inbreeding populations there are much greater discontinuities between populations in both morphological and physiological characters. Nearly continuous intergradation between populations is frequently found in the Hawaiian flora. Hillebrand (1888:xxv) states, "A comparison of the Hawaiian flora with that of any other country brings out at once a striking difference in the great number of varieties in all the species of leading genera." And Fosberg (1948:107) commented, "The reputation for polymorphism

enjoyed by Hawaiian plants has led taxonomists to avoid undertaking major problems on them." Polymorphism, inherent in outcrossing breeding systems, is further evidence for a truly high proportion of outcrossing. The outcrossing has been effected at least partially through dioecism which has developed in at least 14 different families in less than approximately 5,000,000 years.

SUMMARY

It is proposed that Baker's Law has been effective during the development of the Hawaiian indigenous flora. There is no reason to assume differently and there is good support for this view in the present structure of the Hawaiian flora. At the same time it can be demonstrated that there is a significantly higher percentage of dioecism in Hawaii than is found in continental floras. Dioecism is a very effective mechanism for outcrossing and in species in which it occurs there is assurance that an open recombination type is present. While self-incompatibility of hermaphroditic species occurs, the same plant family usually does not show self-incompatibility and dioecism. It is true that dioecism alone is not a measure of outcrossing in a flora since other outcrossing mechanisms occur. However, by estimating dioecism, one knows that outcrossing occurs *at least* as much as would be indicated by the proportion of dioecism. Thus, there is no reason to deny the applicability to the Hawaiian indigenous flora of Baker's Law of self-compatibility and long distance dispersal; yet there is an active outcrossing breeding system at work in Hawaii, where one would expect the contrary. The dilemma can be resolved if we recognize that the dioecious habit can develop relatively quickly and may then be perpetuated if it has greater survival value than hermaphroditism. Several workers have experimentally produced dioecious species or races.

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